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Avian Theory of Mind and counter espionage by food-caching western scrub-jays (*Aphelocoma californica*)

Joanna M. Dally ^a; Nathan J. Emery ^b; Nicola S. Clayton ^a

^a University of Cambridge, Cambridge, UK ^b University of Cambridge, Cambridge, and Queen Mary, University of London, London, UK

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Avian Theory of Mind and counter espionage by food-caching western scrub-jays (*Aphelocoma californica*)

Joanna M. Dally

University of Cambridge, Cambridge, UK

Nathan J. Emery

*University of Cambridge, Cambridge, and Queen Mary,
University of London, London, UK*

Nicola S. Clayton

University of Cambridge, Cambridge, UK

Food-caching scrub-jays hide food for future consumption and rely on memory to recover their caches at a later date. These caches are susceptible to pilfering by other individuals, however. Consequently, jays engage in a number of counter-strategies to protect their hidden items, caching most of them behind barriers, or using shade and distance as a way of reducing what the potential pilferer might see. Jays do not place all their caches in one place, perhaps because unpredictability provides the best insurance against pilfering. Furthermore, after being observed by a potential pilferer at the time of caching, jays re-hide food in new places. Importantly, however, jays only re-cache food if they have been observed during caching and only if they have stolen another bird's caches in the past. Naïve birds that have no thieving experience do not do so. The inference is that jays with prior experience of stealing others' caches engage in experience projection, relating information about their previous experience as a pilferer to the possibility of future cache theft by another bird. These results raise the intriguing possibility that re-caching is based on a form of mental attribution, namely the simulation of another bird's viewpoint.

Keywords: Avian cognition; Corvids; Food-caching; Scrub-jays; Theory of Mind.

Correspondence should be addressed to Nicola S. Clayton, Department of Experimental Psychology, Downing Street, Cambridge CB2 3EB, UK. E-mail: nsc22@cam.ac.uk

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INTRODUCTION

When faced with a novel problem, humans are able to assess whether or not they have the requisite knowledge for its solution. For example, although no two games of cards are ever alike, participants in a one-deck game of poker might assess their chances of winning by considering the cards in their hand, the cards which have been played, and the cards which are still unaccounted for. To do so participants must not only evaluate what they know, but also what others do and do not know, and update this information to inform their future behaviour.

The ability to attribute others with specific knowledge states is a facet of high-level social cognition known as Theory of Mind (ToM). In brief, ToM refers to the ability to attribute other individuals with mental states, such as seeing and knowing, and to know that the mental states of others may differ to your own. Humans are endowed with a unique means of communicating the possession of this cognitive ability, namely language. Consider our poker players: if at the end of the game we were to ask them why they played the cards they did, we would undoubtedly be given a verbal report of the judgements they had made. Even if our players were not adept at remembering which cards others had or had not *seen* being played, and therefore which cards others did or did not *know* about, they might purport to have been successful by basing their game on a “feeling of knowing”.

One of our primary research interests is the extent to which a very different species, the western scrub-jay (*Aphelocoma californica*), is also capable of social cognition. One reason we might expect western scrub-jays to be socially astute is that they are members of the corvid (or crow) family, a group of songbirds that often live in large social groups (Goodwin, 1986). Rather than populations of spatially aggregated individuals, however, corvid social life is typified by a high degree of social complexity (see Clayton & Emery, 2007, for a recent review). For example, rooks and jackdaws are colonial and known to form life-long monogamous pair bonds, with individuals forming long-term alliances with other members of their group, and understanding “third-party” relationships (Emery, von Bayern, Seed, & Clayton, 2007).

While western scrub-jays are generally considered to be semi-territorial, they are often embroiled in prolonged social interactions (Curry, Townsend Peterson, & Langen, 2002). For example, although mated jays commonly defend their territory, pair members frequently interact with neighbouring birds and, outside of the breeding season, tolerate the presence of non-breeders in their territory (Curry et al., 2002). Moreover, like their close relative, the Florida scrub-jay (*Aphelocoma coerulescens*), specific populations of western scrub-jays engage in a system of co-operative breeding where several closely related family members share the

responsibility of raising the young (Burt & Peterson, 1993; Curry et al., 2002). This has led to the speculation that western scrub-jays might have “more complicated social networks than appears superficially” (Curry et al., 2002, p. 18).

The complex social life of primates has been invoked as an explanation for their advanced cognitive abilities (Humphrey, 1976; Jolly, 1966). In the social function of intellect hypothesis, Humphrey (1976) argued that “social primates are required by the very nature of the system they create and maintain to be calculating beings” (p. 309), and went on to liken the strategies involved in social manipulation to the plots and counterplots involved in a game of chess. The capacity for primates to socially manipulate one another has since been termed “Machiavellian intelligence” (Byrne & Whiten, 1988).

While the social function of intellect hypothesis (Humphrey, 1976) was developed to provide a context for the advanced intelligence of primates, Whiten and Byrne (1997, p. 14) subsequently suggested that “an evolutionary selective pressure towards greater social intelligence must surely apply to any species meeting the basic criteria, of living in large, semi-permanent social groups of long lived individuals”. As Clayton, Dally, and Emery (2007) have discussed, these parameters are wholly applicable to corvids. Consequently, we might expect species such as the western scrub-jay to possess socio-cognitive abilities on a par with the great apes. Although this review focuses specifically on the western scrub-jay, we suspect that many other corvids may also possess these complex socio-cognitive skills, and indeed there is very strong evidence to support the case for ravens (e.g., Bugnyar & Heinrich, 2005, 2006; Bugnyar & Kotrschal, 2002, 2004; Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007; see Bugnyar, 2007, for a review).

The notion that a bird may possess ToM, a cognitive ability supposedly unique to humans, may at first sight appear preposterous. Many researchers would argue that if any non-human animal would be predicted to possess ToM or at least the precursors of ToM, surely it would be a chimpanzee (Premack & Woodruff, 1978). But as we have argued, corvids demonstrate cognitive skills on a par with the great apes, and in many cases surpass them, suggesting convergent evolution of intelligence in these two distantly related families (Emery & Clayton, 2004). Until recently, the avian brain was thought to be unable to support complex cognition because the forebrain was largely comprised of areas devoted to species-specific or survival behaviours, such as feeding and mating (e.g., striatum), compared to the largely cortical mammalian forebrain devoted to learning and cognition. However, recent studies of avian neural connectivity, neurochemistry and phylogenetic analyses have found that the avian forebrain is more cortical like than previously thought, with few striatal areas (Jarvis et al., 2004). Indeed, part of the avian forebrain called the nidopallium is structurally, neurochemically and functionally equivalent to the mammalian prefrontal

cortex (Güntürkün, 2005). Furthermore, corvid and ape forebrains are the same relative size (Emery & Clayton, 2004). These new findings therefore provide an empirical neural basis for any suggestion of complex cognitive abilities such as mental time travel, causal reasoning and ToM, as well as executive functions that are processed within the prefrontal cortex of humans, and presumably other apes (e.g., Waltz et al., 2002). We will turn our attention to the question of whether some birds, notably food-caching western scrub-jays, may also possess complex social reasoning skills.

FOOD-CACHING AND SOCIAL COGNITION

When observing jays, Aristotle noted that when “acorns are getting scarce, it [the jay] lays up a store of them in hiding” (translated by Balme, 1991, p. 275). While food-hiding behaviour is by no means unique to jays (Vander-Wall, 1990), Aristotle’s observation encapsulates the idea that sequestering food has evolved to enable the food-cacher to survive periods of temporal food scarcity (Roberts, 1979).

We now know that a number of corvids, including western scrub-jays, not only store food, but also use observational spatial memory to steal caches that they have observed others make (Bednekoff & Balda, 1996a, 1996b; Clayton, Griffiths, Emery, & Dickinson, 2001; Heinrich & Pepper, 1998; Watanabe & Clayton, 2007). Cachers and pilferers (birds who steal others’ caches) can therefore be considered opposing sides of what has been termed an “evolutionary arms race” (Bugnyar & Kotrschal, 2002), a metaphorical race in which the “arms” in question are the tactics that cachers should develop to thwart the pilfering attempts of their competitors, and that pilferers should perfect to facilitate cache theft. Consequently, we might expect individuals to engage in behaviours to outmanoeuvre their conspecifics and maximize their own access to resources. As the same individuals play the dual role of storer and stealer, however, the division between the two sides is far from clear cut.

Protecting hidden caches

While at the University of California Davis, one of us (Clayton) noticed that western scrub-jays commonly took food scraps discarded by humans during their lunch hour and cached them in the surrounding grounds. After hiding their spoils, storsers tended to fly off to a nearby perch and wait. These birds were colour-banded and therefore individually recognizable, and, once other jays had left the scene, it was possible to observe the storer returning to recover their hidden items. Rather than eating their caches, however, the storer would typically move most of the recovered items to new sites. The inference from these field observations is that by re-caching items in new

sites when competitors had left the scene, storers prevented potential pilferers from using observational spatial memory to accurately steal their caches. It is possible, however, that the presence of other birds at the point of caching was coincidental to, and not the motivation for, the storer's re-caching behaviour.

To determine whether re-caching behaviour constitutes a protection behaviour, scrub-jays were presented with two locations in which to cache. As illustrated in Figure 1, top panel, jays cached in one tray while being observed by a conspecific (Observed tray), before caching in the second tray when the observer's view was obscured (In Private tray), or vice versa. Three hours post-caching, the Observed and In Private caching trays were returned to the storer together with a third previously unseen (new) tray, and the birds were allowed to recover their caches. To ensure that the birds' recovery behaviour was dependent on a memory for the social context of the caching episode, as opposed to being guided by behavioural cues from potential thieves, cache recovery always occurred In Private. If re-caching functions as a cache protection strategy, storers would be predicted to re-cache items hidden in the presence of observers, and to move these caches specifically to sites in the new tray as these would be unbeknown to their competitor.

As shown in Figure 1, bottom panel, the jays re-cached significantly more items from the Observed tray relative to the In Private tray (Emery & Clayton, 2001). Furthermore, while the few items re-cached from the In Private tray were placed in new and old sites alike, caches from the Observed tray were moved specifically to sites in the new tray. By re-caching items from the Observed tray in sites unbeknown to prior observers, storers preclude potential thieves from using memory to facilitate cache theft. The results of these experiments therefore accord with those expected if re-caching functions as a cache protection behaviour.

Who is watching

The previous experiment demonstrated that scrub-jays adjust their recovery behaviour as a function of whether or not they were observed during a specific caching event. What is not clear is whether a storer's re-caching behaviour is governed by the presence of a live conspecific at caching, or whether the moving image of a conspecific would be sufficient to motivate the storer to re-cache.

In a second experiment, we allowed our jays to cache food in each of three social contexts; Observed, In Private and in the presence of a mirror. The Mirror condition acted as a control, providing the image of a moving bird without the increased risk of cache theft provided by the presence of a real observer. Cache recovery always took place In Private. The experimental set-up is illustrated in Figure 2, top panel.

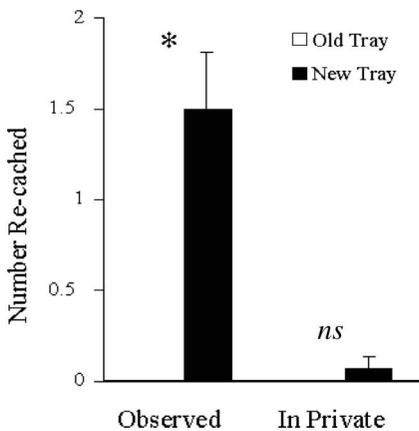
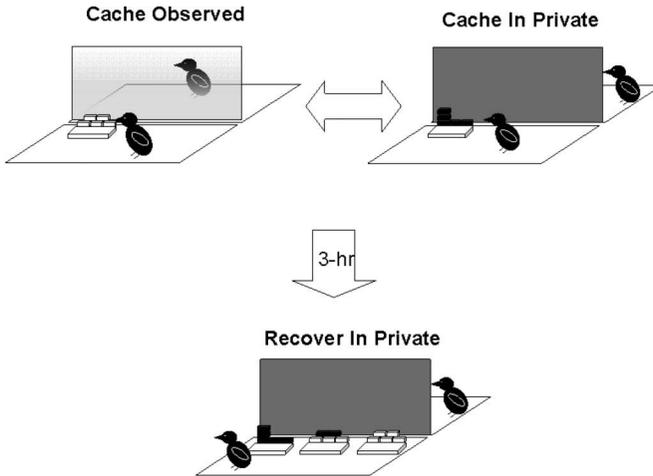


Figure 1. *Top panel:* The experimental set-up of the caching and recovery conditions for the Re-caching experiment. Storers cached in one tray watched by a conspecific (☞=Observed tray) and in a second tray when the observer's view was obscured by an opaque divider (☞=In Private tray). At recovery, which occurred In Private, storers received the trays in which they had previously cached plus one "new" tray (☞). *Bottom panel:* The mean number of items (+ SEM) re-cached in the new and old trays after the Observed and In Private caching conditions. * $p < .05$.

Based on the results of the previous experiment, the birds' recovery behaviour was predicted to differ between the three caching conditions. If the presence of a moving image was sufficient to elicit re-caching behaviour, we predicted that jays should re-cache items at a similar level after caching in the Mirror and Observed conditions and that in both these conditions

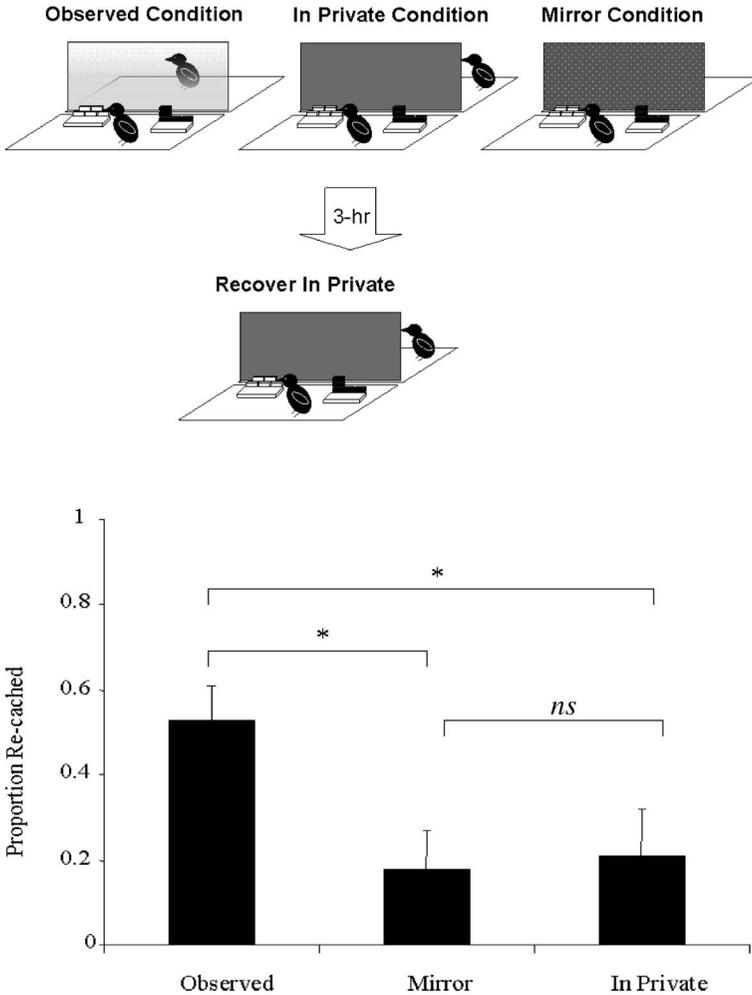


Figure 2. *Top panel:* The experimental set-up for the Mirror experiment. Storsers cached either Observed by a conspecific, In Private, or in front of a mirror. Irrespective of caching condition storsers recovered their caches In Private. *Bottom panel:* The mean proportion of items (+ SEM) re-cached after the Observed, In Private and Mirror caching conditions. * $p < .05$; ns = non-significant.

re-caching should occur at a higher rate than after caching In Private. By contrast, if the presence of a live conspecific is necessary to stimulate re-caching at recovery, the storsers' recovery behaviour after caching in the Mirror condition should be similar to when In Private, but significantly different from when Observed.

As shown in Figure 2, bottom panel, the birds re-cached many items after the Observed condition whereas few items were re-cached after the In Private condition. Intriguingly, the birds' recovery behaviour after the Mirror condition was similar to that exhibited after the birds had cached In Private with few items being re-cached in new and old sites.

A variety of avian species have previously been exposed to their mirror image, and in all but one case their reaction suggested that they treated their reflection as a social stimulus (parrots, *Psittacus erithacus*, Pepperberg, Garcia, Jackson, & Marconi, 1995; jungle crows, *Corvus macrorhynchos*, Kusayama, Bischof, & Watanabe, 2000; towhees, *Pipilo fuscus petulans*, Ritter & Benson, 1934; chickens, *Gallus gallus*, Gallup, 1991). Perhaps it is not at all surprising that the one exception concerns a fellow corvid, the magpie. In a recent study, Prior and colleagues argued that magpies may indeed be capable of recognizing themselves in a mirror, for rather than attacking their mirror image, they pass the mark test, i.e., using the mirror to investigate marks placed on parts of their body they would otherwise be unable to see (Prior, Schwarz, & Güntürkün, 2008).

Our jays, like the magpies and unlike the other avian species that have been subjected to mirror tests, are clearly responding to more than the distinction between the presence and absence of a visual image of another bird, because they did not respond to the mirror image in the same way as a live observer. The birds' re-caching behaviour therefore raises the possibility that scrub-jays, like magpies (Prior et al., 2008) and like the highly encephalized mammals, namely apes (chimpanzees, *Pan troglodytes*, Povinelli et al., 1997; Suarez & Gallup, 1981; orangutans, *Pongo pygmaeus*, Miles, 1994; Suarez & Gallup, 1981) and dolphins (*Tursiops truncatus*, Reiss & Marino, 2001), may recognize that the reflection in the mirror is an image of themselves.

An understanding of "self" has been proposed as a key cognitive skill for monitoring what we do and do not know, a prerequisite for attributing others with knowledge or ignorance, as it requires an assessment based on personally unique information. It is not necessary to invoke a self-concept, however, to explain the differences in the scrub-jays re-caching behaviour in the Observed and Mirror conditions. It is possible that the jays may simply have habituated to the mirror image, and might therefore have ceased to respond to it as a competitor. It should be noted, however, that while the jays had been exposed to a mirror for a period of 12-hours prior to this experiment (Emery & Clayton, 2004), many species fail to habituate to a mirror image even when exposed to a mirror for over 20,000 hours (Anderson, 1983, 1984; Gallup, 1979). Alternatively, the storer might perceive the "conspecific" in the mirror to be preoccupied by their own caching behaviour, and therefore to pose little threat as a potential thief. Indeed, Källänder (1978) noted that rooks storing walnuts were not

secretive if nearby conspecifics were also storing. Finally, like parakeets (*Melopsittacus undulates*) the storer may have differentiated between the live and reflected “observer” because of the perfect contingency between the storer’s own movements and those of the “conspecific” (Gallup & Capper, 1970).

Cache site choice

Irrespective of the specific discrimination being made the results of the Mirror experiment add further support to the hypothesis that scrub-jays engage in re-caching behaviour to minimize cache theft from potential thieves. In the wild, however, waiting until potential thieves are no longer present before engaging in cache protection behaviour may not always be possible, as observers have constant access to the storer’s caches. Perhaps a storer’s most effective tactic would be to cache in sites that others cannot see.

There are three lines of converging evidence to suggest that scrub-jays are sensitive to the visual perspective of potential thieves (what they can and cannot see), and that storers use this information when engaging in cache protection. First, when allowed to cache in two trays, one of which was in view of a potential thief and one of which was positioned behind a barrier such that it was out of view of the observer, jays preferentially cached in sites their competitor could not see (Dally, Emery, & Clayton, 2005a). Second, when unable to cache out of view of potential thieves, jays cached primarily in sites that were, in relative terms, harder for observers to see. For example, when given the opportunity to cache near or far from a conspecific, storers preferentially cached in far sites (Dally et al., 2005a). Similarly, when cache sites differed in that one was well lit and the other in shadow, storers preferred to cache in the “shady” tray (Dally, Emery, & Clayton, 2004). Critically, the birds’ selectivity to cache out of view of conspecifics, or in far or shady sites, was only exhibited when they were observed during caching; when caching occurred In Private all sites were used with indifference. This suggests that storers engage in strategies to prevent or reduce the transfer of visual information to potential thieves during a caching event, a behaviour which might serve to reduce the accuracy with which competitors are able to use memory to locate the storer’s caches.

The final line of evidence to suggest that jays are sensitive to the visual perspective of others comes not from their behaviour at caching but from their behaviour at recovery. As we described earlier, one way in which storers might reduce the likelihood that their caches will be stolen is to re-cache items hidden in the presence of observers when alone. Indeed, after each of the experiments we have just described (Barrier, Distance, Shade), re-caching levels were greatest after the birds had been observed during caching relative to when caching occurred In Private (Dally et al., 2004,

2005a). Particularly pertinent to our current discussion is that during the Observed condition this re-caching behaviour was directed specifically at those sites to which the observer had the best visual access (near, in view, well lit). Because, irrespective of caching condition, cache recovery always occurred In Private these differences in the birds' recovery behaviour must depend on a storer's memory for the social context of caching (i.e., the absence or presence of an observer jay) and the specific attributes of the two trays (i.e., in view vs. out of view). One potential benefit of re-caching items to which prior observers had the best visual access is that those caches most at risk of theft are conferred an additional degree of protection.

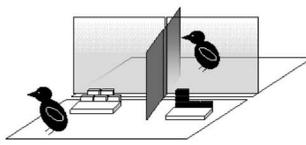
Access all areas

Until now we have focused on the capacity for storing jays to reduce the pilfering accuracy of potential thieves by implementing visually based cache protection strategies. In the wild, however, these tactics might be impractical as potential thieves would be able to constantly reposition themselves in order to maximize their view of a caching event. Indeed, Bugnyar and colleagues found that in the presence of storing conspecifics, ravens often altered their position relative to structures that would have otherwise blocked their view (Bugnyar & Kotrshall, 2002), and actively lead competitors away from the true cache locations (Bugnyar & Kotrshall, 2004), as well as keeping track of knowledgeable and ignorant competitors in their role as both cacher and pilferer (Bugnyar & Heinrich, 2005, 2006).

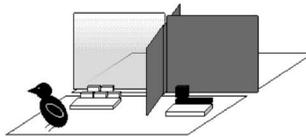
To determine how our jays would cope when the position of observers was unpredictable, we allowed them to cache in two trays in two very different conditions. The first condition was a replicate of the Barrier experiment, in that one of the storer's trays was constantly in view and one constantly out of view of a potential thief (Constrained condition). By contrast, in the Free condition, a partial barrier was placed in the observer's home cage such that the observer could see the tray on the left-hand side of the storer's cage by moving to the left of the barrier (which then occluded the right-hand tray), and the tray on the right of the storer's cage by moving to the right of the barrier (which then occluded the storer's left-hand tray). Consequently, while the observer was potentially able to see both of the storer's trays, it was only able to view one tray at any one moment in time. The experimental set-up is illustrated in Figure 3, top panel.

Irrespective of caching condition storer's preferentially cached when observers were out of view; a finding that accords with that of the Barrier experiment we described previously (Dally et al., 2005a). When caching in the Free condition, storer's recovered their cached items and re-hid them elsewhere. As shown in Figure 3, bottom panel, however, items the observer had seen being cached were not simply moved to a new hiding place and left

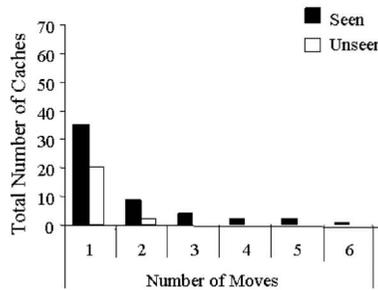
(i) Free condition



(ii) Constrained condition



(i) Free condition



(ii) Constrained condition

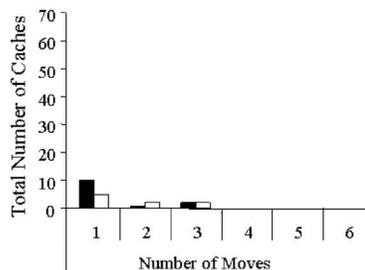


Figure 3. *Top panel:* The experimental set-up for (i) the Free condition and (ii) the Constrained condition (redrawn from Clayton et al., 2007). In the Free condition, the cages of both the storer and observer were partially divided with opaque dividers, which restricted the visual access of both birds to one side of the opposite cage. In the Constrained condition, the storer's cage was partially divided, and the observer's cage fully divided, with opaque screens. The observer therefore had visual access only to one side of the storer's cage. Irrespective of condition, recovery took place in Private (solid dividers attached to both sides of the storer's cage). *Bottom panel:* The total number of times individual caches from seen and unseen sites were moved during the caching period of (i) the Free condition and (ii) the Constrained condition (redrawn from Clayton et al., 2007).

there. Instead, many were moved up to six times, movements that occurred specifically in view of their competitor. By contrast, when cache sites were consistently in view or out of view of potential thieves (Constrained condition), few items were moved.

The repeated movement of caches in the Free condition appears to be a response to the unpredictability of the observer's position, and consequently what they could and could not see. By moving items the observer witnessed being cached, storers might reduce the accuracy with which their competitors are able to relocate hidden caches as the observer's memory for past cache sites should interfere with their memories for the current location of caches. Importantly, storers were able to recover moved and unmoved caches with a comparable degree of accuracy.

In all the experiments we have described thus far, storers have been responding to the *potential* risk posed by an observer. That is, the observer was positioned behind a transparent barrier such that it could not immediately access the storer's caches. Yet in the wild observers would have constant access to the area in which the storer cached. To investigate the caching behaviour of scrub-jays in a more naturalistic context, we placed groups of seven birds into each of three aviaries. Each aviary was provisioned with a bowl of waxworms and the birds caching behaviour observed.

In each aviary, all birds gained access to, and ate from, the bowl of waxworms. Notably, however, only the most dominant male and/or his partner cached (Dally, Emery, & Clayton, 2005b). Like several other corvids, dominant jays used aggression to drive potential thieves away from cache sites (Eurasian jays, *Garrulus glandarius*, Bossema, 1979; Goodwin, 1986; Wilmore, 1977; rooks, *Corvus frugilegus*, Goodwin, 1986). What is of particular interest is that aggressive defence was used in conjunction with another strategy, namely moving caches multiple times.

While the multiple movements of caches appears to represent a cache protection tactic, it may represent little more than an "automatic" response to the presence of mobile observers. Closer analysis of the birds' movement behaviour renders this explanation unlikely, however, as the number of times birds moved caches around on any given trial increased relative to the number of times conspecifics attempted to steal their caches. This suggests that repeated cache movement is expressed flexibly depending on the degree of risk posed by observers.

The risk of cache theft was not the only factor to influence whether or not storers engaged in cache protection behaviour. Although jays aggressively defended cache sites from potential thieves, storers tolerated their partner moving their caches from one site to another. Moreover, partners often aggressively defended one another's caches from pilfering conspecifics. These two lines of evidence suggest that, like ravens (Heinrich & Pepper, 1998), scrub-jays do not perceive their partner to pose a risk to cache safety.

To investigate the effect of social relationships on the propensity for jays to engage in cache protection tactics, we conducted a replicate of the Distance experiment. In this study, storers were once again given the opportunity to cache in each of two trays, one of which was further from an observing conspecific than the other. To determine whether a storer's social relationship with an observer impacted upon their caching behaviour, birds cached in each of four conditions; observed by their partner, a dominant bird, a subordinate bird or In Private.

Intriguingly, the birds engaged in a distance strategy in the Dominant and Subordinate conditions but did not do so after caching in view of their partner or In Private (Dally, Emery, & Clayton, 2006). Moreover, during a private recovery period, storers re-cached items hidden in the tray to which the observer had the best visual access (near tray) after caching in view of a subordinate or a dominant bird. Yet no such preference was exhibited if the cacher hid the caches in view of their partner. Cachers also appeared to differentiate between the relative risk the subordinate and dominant birds posed to their caches, as re-caching levels were highest after caching in view of a dominant bird suggesting they do not perceive their partner to pose a risk to cache safety (Dally et al., 2006).

Assessing observer risk

The jays' behaviour in the aviary study provided some insight into the cache protection behaviour of jays in a group situation. In the wild, however, the same birds might not always be present at caching and recovery. For example, some observers might leave the area in which a storer cached only to be replaced by previously absent conspecifics. Consequently, a storer might become surrounded by birds that had, or had not, witnessed a prior caching event. Our most recent experiment provided an analogue of this situation (Dally et al., 2006). Specifically, storers were given the opportunity to cache in the presence of two different observers in two consecutive caching events, and then to recover their caches either when In Private, watched by one of the prior observers (Observed condition), or watched by a naive bird that had not witnessed either caching event (Control condition). The experimental design is shown in Figure 4, top panel.

As predicted by our previous findings, storers re-cached hidden items in new sites when they recovered their caches In Private. By contrast, in the Observed condition, storers moved caches the observer at recovery had seen them make multiple times. This result accords with the birds' behaviour in two earlier experiments (Free vs. Constrained experiment and the aviary study; Dally et al., 2005a, 2005b) in which storers were unable to engage in behaviours that conferred their caches with a degree of visual protection. As shown in Figure 4, bottom panel, items that the observer at recovery had not

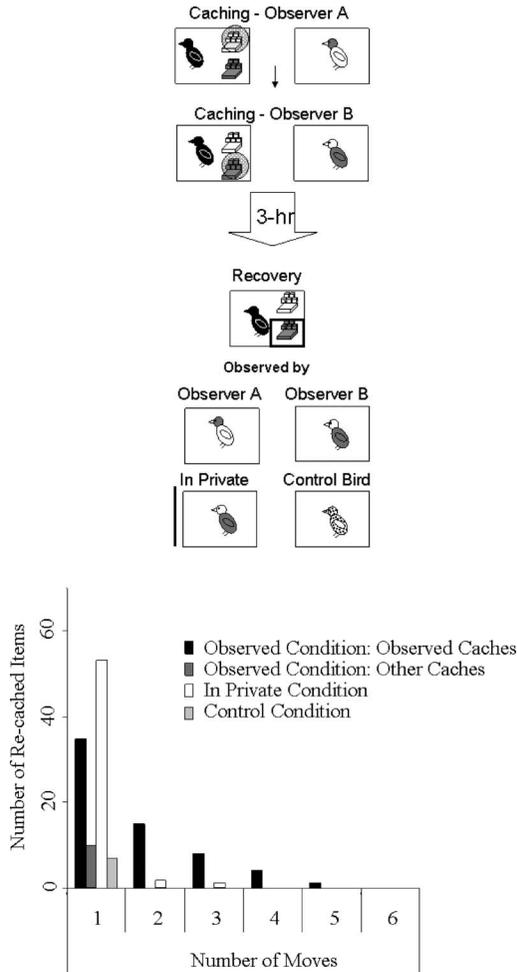


Figure 4. *Top panel:* The caching and recovery conditions of the “who was watching” experiment. = storer, = observer A, = observer B, = control-observer, = Perspex strips, = “observed” tray (redrawn from Clayton et al., 2007). *Bottom panel:* The total number of times individual caches were moved from the observed and other trays in the Observed condition, and from both trays during the Control and In Private conditions.

seen cached were rarely moved, a finding illustrated most clearly by the storers’ propensity to move very few items during the Control condition. Indeed, moving caches observers had not witnessed being cached, would only have served to provide currently uninformed observers with the observational information necessary to facilitate accurate cache theft.

These findings may be taken to suggest that the jays' are capable of one of the key skills of high-level social cognition, understanding what others do and do not know, and that they remembered *who* saw *which* caches being hidden and took appropriate action to protect their caches during a subsequent recovery period. A simpler explanation is that storers may have responded to behavioural cues exhibited by the potential thief. Consider the storers propensity to repeatedly move caches the observer at recovery had witnessed being hidden. It is possible that this behaviour constituted a response to the observers' propensity to preferentially attend to sites in which they had observed items being cached, and to spend little time attending to the tray in which they had not observed the storer cache.

To determine whether scrub-jays differentiate between observers on the basis of what they do and do not know, or whether they simply responded to behavioural cues exhibited by the observer, we ran a further experiment (Dally et al., 2006). This experiment comprised an Observed condition, a direct replicate of the Observed condition in the previous experiment, and an Observer-Control condition (Figure 5, top panel). The two conditions were similar in that storers cached successively in two trays, each in view of a different observer. In the Observer-Control condition, however, a control-observer also witnessed a control-cacher caching in one of the two trays. Consequently, two observers and one control-observer had each witnessed food being hidden in one of the two trays. At recovery, both observer and control-observer saw a storer (not a control-storer) recover its caches. As a result, storers in the Observed condition were observed by the same observer at caching and recovery, whereas storers in the Observer-Control condition, cached in view of an observer, but recovered their caches in the presence of the control-observer.

Based on the previous experiment, we predicted that cachers in the Observed condition would predominantly re-cache items from the tray in which the observer at recovery had seen them cache (observed tray) and not from the other tray. If this re-caching behaviour represents a capacity for social cognition, storers should re-cache few items from either tray in the observer-control condition, because the control-observer was not present when the storer cached and is therefore ignorant of the location of cache sites. If, however, storing birds base their recovery behaviour on behavioural cues emitted by competitors (e.g., differences in the degree to which observers attend to sites they have and have not observed being cached in) storers should re-cache items from the observed tray in both conditions, as although the control-observer was not present when the cacher cached, it would be attending to the tray in which it had previously observed the control-storer cache.

As shown in Figure 5, bottom panel, the birds' behaviour was consistent with a cognitive explanation, and not with an explanation based in terms of

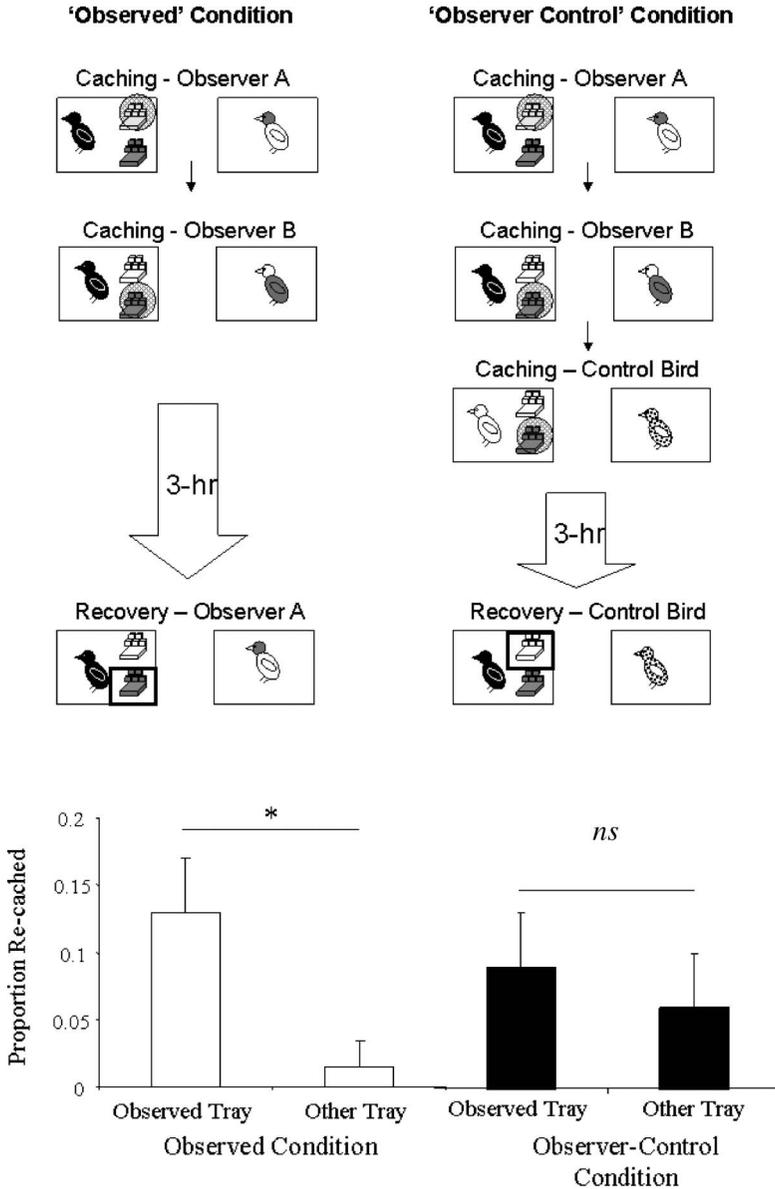


Figure 5. *Top panel:* The experimental set-up of the “Observed” and “Observer-Control” conditions. = storer in “Observed” and “Observer-Control” conditions, = control-storer, = observer A, = observer B, = control-observer. = Perspex strips, = “observed” tray (redrawn from Clayton et al., 2007). *Bottom panel:* Mean proportion (+ SEM) of items re-cached from the “observed” and “other” trays in the “Observed” and “Observer-Control” conditions. * $p < .05$; ns = non-significant.

behavioural cueing. In the Observed condition, items were predominantly re-cached from the tray in which the observer at recovery had seen them cache, whereas both trays were treated alike in the Observer-Control condition.

Our findings suggest that scrub-jays remember who was present during particular prior caching events, and use this information when engaging in behaviours to minimize cache theft. At first glance, this behaviour appears to necessitate the birds to be able to attribute their conspecifics with unobservable states such as “knowing”. It is necessary to point out, however, that rather than requiring a human-like “theory-of-mind”, the birds’ behaviour may have arisen from a combination of behavioural predispositions and conditional discriminations.

Theory of Mind and experience projection

In a social environment, the outcome of any given interaction depends not only on your own behaviour, but also on the behaviour of others. The capacity for attributing others with knowledge states appears to represent a cognitive cornerstone in predicting how others might behave. Indeed, we have suggested that food-caching jays might tailor their use of cache protection behaviours to reflect a competitor’s knowledge state (Dally et al., 2006). Yet in humans, social behaviour is shaped not only by the events of the present, but by the consequences of past experiences.

To investigate whether scrub-jays were able to draw upon the experiences of their past to mitigate a socially induced problem, that of cache theft, Emery and Clayton (2001) allowed two groups of jays to cache either Observed or In Private and to recover their caches three-hours later In Private. Critically, only one of these two groups had prior experience of stealing others’ caches.

As predicted by the “Re-caching” experiment we described earlier, jays only re-cached hidden items after being observed during caching, and re-cached items were placed specifically in new sites. Critically, however, this re-caching strategy was specific to birds that had previously been thieves. Birds without this experience consistently failed to re-cache many items, irrespective of having previously cached in view of observers or of witnessing cache theft, and those few items that were re-cached were often placed in old sites (Figure 6).

The finding that storers need first-hand experience of pilfering the caches of others in order to know which items to re-cache, and where to re-cache them, suggests that scrub-jays are capable of a high level of social understanding called “experience projection” (Emery & Clayton, 2004). Specifically, storers appear to relate information about their previous experience as a pilferer to the possibility of future theft by another bird, and

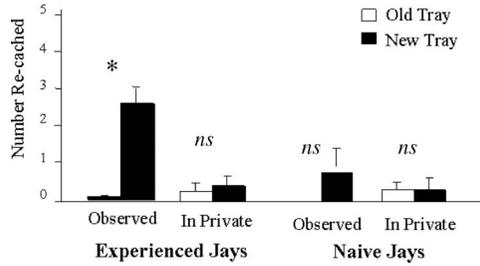


Figure 6. The mean number (+ SEM) of items re-cached in new and old sites at recovery after the Observed and In Private caching conditions for (left) birds that had previously stolen the caches of others (experienced birds), and (right) birds that had not experienced stealing others' caches (naïve birds). * $p < .05$; ns = non-significant.

adjust their recovery behaviour to ameliorate the effects of the thieving behaviour in which they previously engaged.

CONCLUSION

Common to all the cache protection behaviours we have discussed is that they function to reduce the quality of a competitors' informational, or epistemic, environment. For instance, by caching in sites that conspecifics cannot see, storing jays prohibit informational/knowledge transfer to their competitor. Yet the jays not only act to reduce a conspecifics access to factual information (i.e., cache location), but they also engage in behaviours that function to misrepresent the informational environment. This ability to "muddle" the epistemic environment of competitors (Proust, 2006), is perhaps best evidenced by the jays' propensity to re-cache hidden items when prior observers are no longer present, resulting in potential thieves being misinformed as to cache location.

When considering behaviours that function to muddle the epistemic environment, it is immediately apparent that they need not be underpinned by any form of complex socio-cognitive process. Consider the propensity for plovers to perform a broken-wing display in the presence of a predator (Ristau, 1991). Rather than an intentional act to draw a knowledgeable competitor away from their nest, the plovers display might simply represent a response to the stimulus "predator". The use of cache protection behaviours by scrub-jays cannot be explained in such terms, however. Instead, the finding that tactics are employed flexibly, as a consequence of the cacher's social relationship with the competitor, the likelihood of cache theft, and the specific caching episodes the observer has witnessed, suggests that the birds' behaviour is grounded in social cognition. Moreover, the finding that jays appear capable of experience projection, using their own

past experience of being a thief to predict how another individual might behave in the same situation, provides evidence for a form of Theory of Mind yet to be demonstrated in any of the great apes, other than humans.

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